FOSSIL REPTILES FROM ALDABRA ATOLL, INDIAN OCEAN
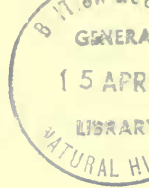
BY

EDWIN NICHOLAS ARNOLD

BRITISH MUSEUM (NATURAL HISTORY)

Price £2·25

FOSSIL REPTILES FROM ALDABRA ATOLL, INDIAN OCEAN

By E. N. ARNOLD

CONTENTS

SYNOPSIS

The present reptiles of Aldabra comprise only the giant tortoise, *Geochelone gigantea*, two geckoes, *Phelsuma abbotti* and *Hemidactylus mercatorius*, and the skink, *Cryptoblepharus boutonii*, but a richer and quite different fossil fauna has recently been discovered. Giant tortoises occur in most terrestrial deposits on the atoll and remains of crocodiles and lizards have been found in two: the Bassin Cabri Calcarenites (undated, but considerably older than 125 000 years B.P.) and cavity fillings in the Aldabra limestone at Point Hodoul formed since 100 000 years B.P. The Bassin Cabri Calcarenites contain remains of a crocodile similar to *Crocodylus niloticus* and of an iguanid lizard of the genus *Oplurus*. These also occur in the Point Hodoul deposits together with five other kinds of lizards, two or three of which are geckoes (a *Paroedura* similar to *P. sanctijohannis* and *P. stumpffi*, a *Geckolepis* close to *G. maculata* and what is possibly a *Phelsuma*) and two skinks (a 'Scelotes' similar to 'S.' *johannae* and a *Mabuya* very like *M. maculilabris*). The Point Hodoul lizard remains may be the food residue of a predator, perhaps an owl. The reptile fauna of Aldabra is much more similar to that of Madagascar and the Comores

Islands than to that of East Africa or of the Seychelles. Composition of the Point Hodoul fauna and the presumed requirements of some of its members suggest that conditions on Aldabra at that time may have been rather similar to those now occurring on the Comores. It is likely that the ecological requirements of the fossil forms were sufficiently different for them all to be able to coexist. Some of the fossils clearly differ in size from their closest modern relatives, both the *Geckolepis* and the *Oplurus* being very large ; possible reasons for this are discussed. Aldabra was completely submerged after the laying down of the Bassin Cabri Calcarenites, but not since the Point Hodoul deposits were formed. Extinction of the reptiles found in the latter may have been largely caused by transient or permanent loss of ecological resources, although competition from the species existing on the atoll today could have been a minor factor. The possible importance of invading predators is difficult to assess. All the reptiles known from Aldabra seem to have been well adapted to the problems of transmarine colonization. There is evidence that the giant tortoises reached the island three times and the crocodile and *Oplurus* at least twice.

INTRODUCTION

THE study of island faunas has had a long history and is again fashionable, one of the most influential events in bringing this about being the appearance of *The theory of island biogeography* by MacArthur and Wilson in 1967. Among the topics that have recently received attention is the problem of what factors limit the number of species on islands and the importance of extinction rates in this process. A restriction on such investigations is the paucity of direct evidence of natural faunal change on islands. This is especially true in the case of reptiles. Instances are known where late Pleistocene or more recent island reptiles have become extinct (see, for instance, Etheridge, 1964, 1965, 1966 for the West Indies, Bravo, 1953 for the Canary Islands and Vinson & Vinson, 1969 for the Mascarenes), but often only part of the previous fauna has disappeared and there is frequently circumstantial evidence that human influences have been important in bringing such changes about. Situations where there has been an extensive faunal turnover in probably more natural conditions would consequently be of interest. Aldabra appears to be a case in point.

Aldabra is situated about 640 km east of the African mainland, about 380 km northeast of the Comores Islands and some 420 km northwest of Madagascar (see Fig. 1). It is a low atoll, being only about 10 m above sea level at its highest point, and is some 34 km long by 14·5 km wide. There is a large central lagoon and the total land area is 155 km². Much of the present surface consists of coral limestone, which is often covered by scrub. There are few natural large trees and the lagoon is fringed by mangrove. The present reptile fauna consists of giant tortoises (*Geochelone gigantea* Schweigger, 1812), two geckoes (*Hemidactylus mercatorius* Gray, 1842 and *Phelsuma abbotti* Stejneger, 1893) and the skink, *Cryptoblepharus boutonii* (Desjardins, 1831). None of these species is confined to the atoll and all of them have relatively wide distributions in the West Indian Ocean.

The island has been the subject of considerable scientific research by a series of expeditions organized by the Royal Society since 1966. Some of the results of this work have been published and a number of papers on the atoll form volume 260 of *Philosophical Transactions of the Royal Society of London, series B* (1971). Braithwaite, Taylor & Kennedy (1973) have given an account of the depositional and
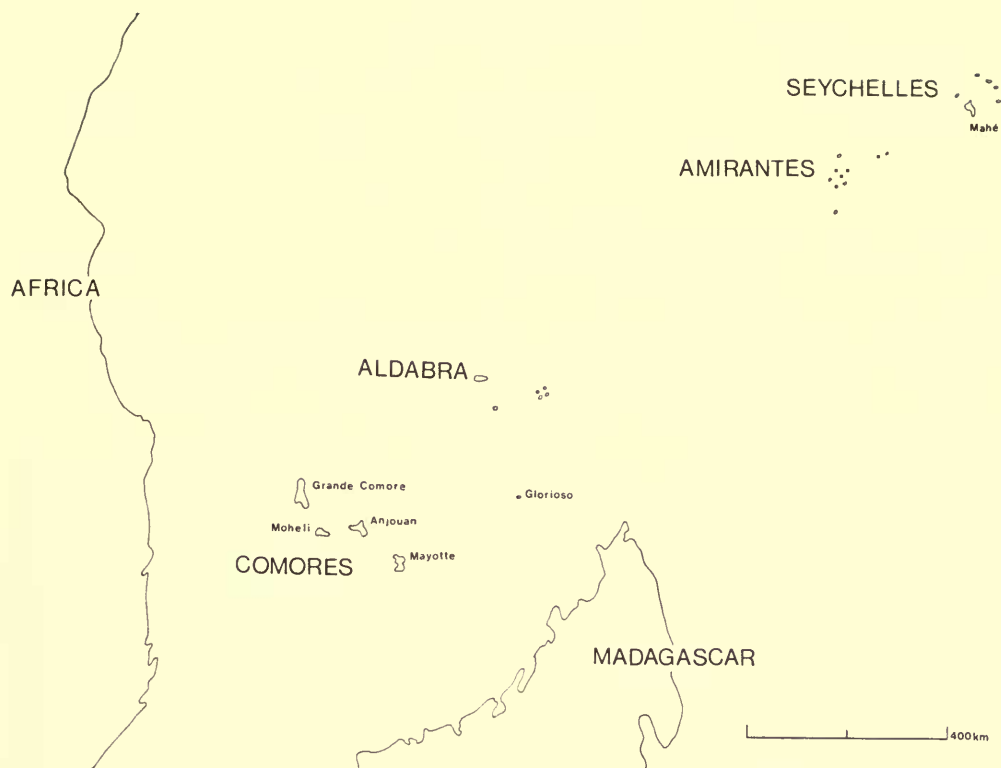
FIG. 1.   West Indian Ocean, showing position of Aldabra and other nearby islands mentioned in text.

erosional history of Aldabra.   During investigations on the island, Dr J. D. Taylor of the British Museum (Natural History) collected substantial amounts of fossil material including the reptiles that form the basis of this paper.   Large numbers of tortoise remains were also observed *in situ* but could not be extracted for detailed examination.

Tortoises occur in many of the terrestrial deposits of Aldabra (Braithwaite *et al.*, 1973).   Lizards and crocodiles have also been found, but only in two deposits, the Bassin Cabri Calcarenites and cavity fillings in the Aldabra Limestone at Point Hodoul (see Fig. 2).   The Bassin Cabri Calcarenites are of unknown age, but they are older than the Aldabra Limestone which has yielded dates by the ^{230}Th/^{234}U method of 118 000 to 136 000 ± 9000 years B.P. (Thompson & Walton, 1972).   The Point Hodoul deposits were probably formed since 100 000 years B.P. (Braithwaite *et al.*, 1973).   Most of the reptile fossils consist of dissociated bones, few of which are intact.   However, although many are broken, the majority are not obviously eroded and are therefore identifiable.   This is especially true of the lizard bones, over 1000 of which have been determined.

FIG. 2. Aldabra Atoll, showing the two main localities where fossil reptiles were collected.

Because of the relatively recent age of the deposits, it was assumed as a working hypothesis that the species represented would probably have close relatives amongst the extant reptiles of the West Indian Ocean, or of the Ethiopian region as a whole. Initial identification was consequently attempted by comparison with the present fauna of that area and it proved possible to find good matches for nearly all the material by this means. Two difficulties in assessing the fossils were the lack of really adequate comparative material in museum collections and the need for taxonomic revision of some of the groups concerned (for instance, the scincine lizards of Madagascar and nearby islands – see Greer, 1970b). These constraints have limited the preciseness of identification in some cases.

As nearly all the fossils are generally like known modern forms, they are not described in detail below. Instead, comment is restricted to diagnostic characters and to any features in which the fossils differ from their modern counterparts. In most cases, the names used for lizard skull elements follow Oelrich (1956). Because many of the fossils are broken, numbers of particular bones, given in the lists of material examined, tend to be minima.

Order TESTUDINES
Chelonians

Family **TESTUDINIDAE**
Land tortoises

GEOCHELONE Fitzinger, 1835

MATERIAL REFERRED. *Point Hodoul cavity fillings.* *Registered number* : R8762. Numerous fragments, especially eroded limb bones.

Tortoise remains were observed in nearly all the terrestrial deposits on Aldabra.

IDENTIFICATION. This material has not been examined in detail, but it resembles *Geochelone gigantea* (Schweigger, 1812), the giant tortoise that occurs on Aldabra at the present time.

Order CROCODYLIA
Crocodilians

Family CROCODYLIDAE
Crocodiles

Crocodylus Laurenti, 1768

MATERIAL REFERRED. *Bassin Cabri Calcarenites. Registered number*: R8885. Tooth: 1.

Point Hodoul cavity fillings. Registered number: R8763–98. Premaxillae: right – 2, left – 1. Maxilla: 1 (fragment). Jugals: right – 5, left – 6. Frontals: 3. Frontal+parietal: 1. Parietal: 1. Parietal+supraoccipital: 1. Squamosals: right – 4, left – 1. Pterygoids: right – 1, left – 1. Ectopterygoids: right – 1, left – 2. Dentary fragments: 11. Isolated teeth: 6. Vertebrae: 2 (fragments). Caudal chevrons: 2. Osteodermal scutes: 45.

IDENTIFICATION. The Point Hodoul remains include premaxillae. These show a clear lateral notch that in life would have received the enlarged fourth mandibular tooth. The bones also suggest that the animals from which they came had snouts that were neither conspicuously narrowed nor laterally expanded. Amongst recent crocodilians, this combination of features is restricted to *Crocodylus*. Comparison of the two extant African species of the genus shows that the fossils are very similar to modern *C. niloticus* Laurenti, 1768, although some elements, e.g. the jugals, appear more robust than those of equivalent-sized mainland African animals with which they were compared. On distributional grounds, *C. niloticus* is the most likely modern crocodile to have reached Aldabra, for it is the only species in eastern Africa. It is also known to have been present in the Seychelles and exists on the Comores and on Madagascar.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. On the basis of the commonest element, viz. the jugal, there must have been at least six individuals represented in the Point Hodoul sample.

ESTIMATED BODY SIZE. Comparison of the fragments with intact skulls of modern African specimens suggests that the largest came from crania about 310 to 320 mm in length (snout-tip to medial posterior border of the supraoccipital bone). Bellairs (1969) has found that the ratio of skull length to total length is about 1 : 7·5 in *C. niloticus* and that this holds over a wide variety of sizes. On this basis, the largest Aldabra fragments would have belonged to an animal 2·33 to 2·40 m long. This is much smaller than the known maximum for mainland African populations, although obviously the small sample available cannot exclude the possibility that the Aldabra animals grew bigger. However, the robustness of some of the bones could indicate maturity and if this is so, the atoll population may have been characterized by small body size. This would not be unexpected, especially as 'dwarf' populations of this species are known from some areas of East Africa (Cott, 1961).

Suborder SAURIA
Lizards

Family GEKKONIDAE
Geckoes

Paroedura Günther, 1879

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number* : R8849–77. Premaxillae : 18. Maxillae : right – 25 (one complete), left – 21. Conjoined nasals – 4. Prefrontals : right – 18, left – 16. Frontals : 28. Postfrontals : right – 23, left – 15. Parietals : right – 11, left – 17. Pterygoids : right – 11, left – 13. Quadrates : right – 21, left – 19. Dentaries : right – 21, left – 18. Coronoids : right – 16, left – 12. Proximal jaws : right – 14, left – 14. Axis : 1. Cervical vertebrae : 10. Dorsal vertebrae : 86 approx. Sacrum : 1. Basal caudal vertebrae : 22. Autotomic caudal vertebra : 1. Scapulocoracoids (incomplete) : right – 1, left – 3. Scapulae : left – 1. Pelvic girdles (incomplete) : right – 9, left – 7. Humeri : more or less intact, right – 1, left – 1 ; proximal sections, right – 13, left – 6 ; distal sections, right – 12, left – 6. Femora : proximal sections, right – 18, left – 21 ; distal sections, right – 7, left – 7. Tibiae : right – 6, left – 3.

IDENTIFICATION. Certain elements of this material are clearly of gecko origin. The frontals, which are undivided, have lateral downgrowths that meet and fuse ventrally to form a cylinder and the vertebrae are amphicoelous. Amongst lizards, both these features are confined to the Gekkonidae, although not universal in them.

Other striking characteristics of these fossils include the following : heavy ossification of the dorsal skull bones ; presence of a well developed, 'sculptured' ornamentation of their outer surfaces ; conjoined nasal bones and prominent notching of the anterior lateral edges of the parietals to take the posterior section of each postfrontal. Within the geckoes, this combination of characters seems to be limited to nine nominal species now confined to Madagascar and the Comores Islands. These have usually been included in *Phyllodactylus* Gray, 1828, but Dixon & Kroll (1974) have recently transferred them to a separate genus, *Paroedura*. As the species concerned do appear to form a natural assemblage, this course is followed here, although the authors' implication that *Paroedura* may have had a separate origin from *Phyllodactylus*, as they understand it, and that the two groups evolved similar foot structure independently is unproven. It seems just as likely that *Paroedura* is a derivative of the more typical members of *Phyllodactylus*.

Paroedura is a quite tightly knit group of species, the interrelationships of which have not yet been fully worked out. This makes it difficult to decide with certainty which of the modern forms are most closely related to the fossil Aldabra material, but the latter has most superficial likeness to *P. sanctijohannis* Günther, 1879 of the Comores Islands and *P. stumpffi* (Boettger, 1878) of North Madagascar and Nossi Bé. It resembles the former closely in the degree and pattern of sculpturing on the dorsal skull bones, in parietal shape (distinctly curved transverse section that is convex above and a distinctly sinuous posterior border) and in having very broad quadrate

bones. However, the frontals are less obviously concave above than in the modern specimens of *P. sanctijohannis* examined (from Anjouan and Grande Comore) and in this respect are more like *P. stumpffi*, although the fossils resemble this species less in details of parietal shape and sculpturing. *P. gracilis* (Boulenger, 1896) is also rather similar, but its parietal has a straighter posterior border and its frontal is more deeply concave above. *P. picta* (Peters, 1854) has a much narrower quadrate and rather coarser 'sculpturing'. The 'sculpturing' in *P. androyensis* (Grandidier, 1867) also seems to be coarser than in the fossils and the parietal is more rectilinear with a flatter transverse section. *P. bastardi* (Mocquard, 1900) shares the latter feature and its 'sculpturing' is coarser still; also the crest on the proximal anteroventral face of the humerus, for the pectoralis muscle, is set almost at right angles to the ventral face of the bone and its anterior face is slightly concave with a well developed anterodorsal ridge forming its upper border. In *P. oviceps* (Boettger, 1881) the parietal is flatter than in the Aldabra material with a less sinuous posterior border and its surface sculpturing is weaker.

Of the two remaining nominal species of *Paroedura*, the unique type of *P. homalorhina* (Angel, 1936) no longer exists (J. Guibé, personal communication) and *P. guibae* Dixon & Kroll, 1974 has not been examined by me.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. There are 28 recognizable frontal bones of *Paroedura*, so at least this number of individuals must be represented in the sample.

ESTIMATED BODY SIZE. On the basis of comparison of limb bones and frontals, it seems that the Aldabra *Paroedura* grew to about 60 mm from snout to vent, or a little more. This compares with a maximum length of 70 mm for modern *P. stumpffi* and 67 mm for *P. sanctijohannis* (see Angel, 1942).

Geckolepis Grandidier, 1867

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number* : R8828–48. Premaxillae : 3. Maxilla : left – 1. Prefrontals : left – 3. Frontals : left – 1 (anterior section only). Parietals : right – 2 fragments (anterior lateral section, central lateral section), left – 3 fragments (2 central lateral sections, posterior lateral section). Palatine : left – 1. Pterygoids : right – 1 fragment, left – 4 fragments. Quadrates : left – 2. Dentaries : right – 1 (anterior section only), left – 1 (anterior section absent). Coronoids : right – 1, left – 1. Vertebral centra : 5. Sacrum : 1. Scapulocoracoids : right – 2, left – 2. Pelvic girdles : right – 2, left – 1. Humeri : more or less intact, right – 1 ; shafts, right – 4, left – 2 ; proximal section, left – 1 ; distal section, left – 2. Femora : proximal section, left – 2 ; distal section, right – 2, left – 2.

IDENTIFICATION. These fragments come from a gecko considerably larger than the Aldabra *Paroedura* discussed above. Initial tentative allocation to the Gekkonidae was based on a number of suggestive, but not fully diagnostic features, for instance the dentary is lightly built with a closed Meckel's groove and a very rounded

lingual face. But, because the remains are so fragmentary, definite family assign-
ment really depends on their detailed resemblance to a particular gecko species.

The more distinctive features of the material are as follows :

1. The largest premaxilla has an estimated 13 teeth. The nasal process is rather
broad and is slightly constricted at the level where it would pass between the external
nasal openings of the skull, but it expands again above this. In the most complete
premaxilla, the process then rapidly tapers to an obtuse point.

2. The maxilla has a broad palatal shelf and the nasal process (i.e. the dorsally
directed lamina that forms part of the side of the snout) rises smoothly from the
tooth-bearing body of the bone with no pronounced inward 'step' just anterior to
the orbit.

3. The anterior lateral fragment of the parietal is peculiar in that the angle between
the fronto-parietal suture and the anterior section of the lateral margin of the bone
is more than a right angle, whereas in most geckoes it is less (see Fig. 3).

4. From the fragments available, it is apparent that the upper surface of each
parietal is distinctly convex above the descending flange of this bone, but lateral to
this it is slightly concave. The convexity extends as a poorly defined ridge that
curves inwards and backwards towards the posterior midline of the skull. From

A   B
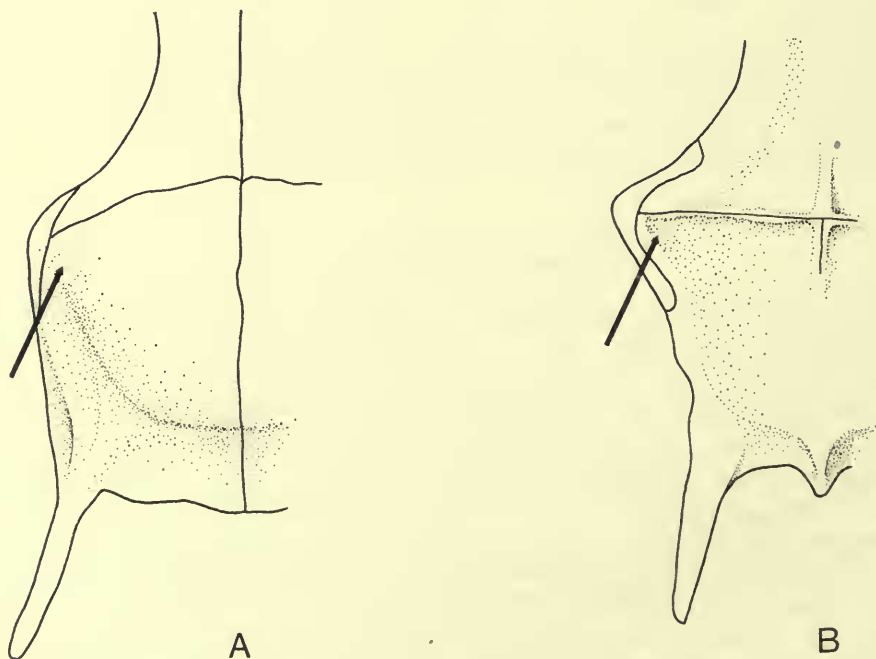
FIG. 3. Dorsal views of the left posterior areas of two gecko skulls, showing difference in
shape of the anterolateral region of the parietal (arrowed). A. *Geckolepis maculata*
(based on BM 91.6.30.1). B. *Homopholis fasciata erlangeri* (based on BM 1931.7.20.255).

this ridge, an even less prominent one runs along the proximal upper surface of the supratemporal process of the parietal.

5.   The outer surfaces of all the fragments of the superficial bones of the skull are either smooth and unornamented, or they have a weak pattern of shallow, thin grooves.

6.   The quadrates have a very slender posterior crest. This is quite strongly and evenly curved (more so than in Aldabra *Paroedura*).

7.   The anterior upper border of the ilium does not rise very abruptly, or recurve forwards, as it does in many geckoes.

8.   The humerus is more robust than in the majority of geckoes. The crest on the proximal anteroventral surface of this bone is set almost at right angles to the ventral surface and its anterior exposure is strongly concave.

Examination of a wide range of Ethiopian and West Indian Ocean gekkonid lizards shows that this combination of features is approached closely only in the genus *Geckolepis*, which is now restricted to Madagascar and the Comores. The apparently related genus, *Homopholis* Boulenger, 1885, differs in having a distinct 'step' in the outer surface of the maxilla, just anterior to the orbit. Also, the fronto-parietal suture of *Homopholis* forms an acute angle with the anterior lateral edge of the parietal bone and there is no concavity on the forward surface of the proximal anteroventral crest of the humerus (all features confirmed on specimens of *H. walbergii* (Smith, 1849) and on *H. fasciata erlangeri* Steindachner, 1906 ; presence of a maxillary 'step' and the shape of the parietal were also checked on the type of *H. heterolepis* Boulenger, 1896). The more distantly related, widespread West Indian Ocean genus *Phelsuma* Gray, 1825 also differs in parietal shape. Furthermore, the premaxilla usually has a slender nasal process, the palatine shelf of the maxilla is typically rather narrow, the quadrate is usually more robust and the anterior upper border of the ilium rises abruptly or is recurved.

Within *Geckolepis*, the Aldabra material was compared with the largest extant species, *G. maculata* Peters, 1880 of Madagascar and the Comores, and with three of the four remaining species, all of which are restricted to Madagascar, viz. *G. anomala* Mocquard, 1902, *G. polylepis* Boettger, 1893 and *G. typica* Grandidier, 1867. Of these, it resembles *G. maculata* most closely. However, the fossils exhibit some mainly minor differences from the small sample of *G. maculata* available for comparison (n = 3) ; these are listed below :

1.   The Aldabra fragments are distinctly larger than corresponding elements in modern *G. maculata*.

2.   The nasal process of the premaxilla is slightly more constricted at the level where it would pass between the external nasal openings of the skull.

3.   In modern material examined, the inner surface of the dentary swings slightly, but clearly, upwards from the base of the tooth-row before curving downwards to form the lingual surface of the bone. In the fossil dentary sections, the upward swing is less marked.

6**

4.   The anterior upper edge of the ilium curves upwards rather less than in compared modern material.

5.   The crest on the proximal anteroventral surface of the humerus is better developed and its anterior exposure is more strongly concave.   Also, the bone is more precisely moulded.

6.   This is true of the proximal section of the femur as well.   In addition, the femoral head has a more pronounced neck which has better developed ridges on its posterior and ventral surfaces.

It is possible that some or all of differences 2 – 6 are merely allometric concomitants of larger size.   If they were due to allometric change, it might be expected that trends towards the conditions found in the Aldabra material would be apparent in a series of modern *Geckolepis* of increasing size, although absence of such trends could merely mean that the changes would only begin to be apparent at sizes larger than those attained today.   In fact, only the expected changes in the humerus can be detected in the small series of *G. maculata* and *G. anomala* available.   Another less direct indication that allometric growth might be responsible for some of the characters of the fossils would be the presence of similar differential growth processes in a related form that grows as large as the Aldabra animals.   When *Homopholis walbergii* of assorted sizes were examined, changes in the femur similar to those expected in *Geckolepis* were found.

Although the features of the humerus and femur that distinguish the fossil *Geckolepis* of Aldabra from modern *G. maculata* may be due to allometric change, there is no evidence that the other characteristics of this material (i.e. differences 2–4) are due to this factor.   However, they are relatively trivial and on their own, or even in conjunction with greater body size, do not seem to provide adequate grounds for recognizing the Aldabra material as a distinct form, especially as the sample of modern *G. maculata* available is so small and the Aldabra remains are so fragmentary.

Estimated number of individuals in sample.   There are five right humeri, the commonest element present.   But there is also a distal section of a left humerus that is smaller than any of the right ones, so at least six individuals must be represented.

Estimated body size.   Calculations based on the sizes of fossil humeri and femora, compared with those of modern animals, suggest that the largest fossil *Geckolepis* were 90 to 100 mm from snout to vent.   This contrasts with a present apparent maximum of 70 mm (Angel, 1942).   .

? *Phelsuma* Gray, 1825

Material referred.   *Point Hodoul cavity filling.   Registered number* : R8878. Maxilla : left – 2 fragments (anterior section, section from just below lachrymal area).   Dentaries : right – 1 fragment, left – 1 fragment (both from middle of bone).

Identification.   The dentary fragments are lightly built and pleurodont with closed Meckel's grooves.   The cylindrical body of the bone shows little dorsoventral

taper along its length, its lower edge is almost straight and the lingual face is strongly rounded. The labial wall extending upwards from the dentary cylinder is very high compared with the depth of the latter and the labial face of the bone has a strongly curved transverse section. On this face, the mental foramina are situated considerably nearer the upper than the lower border of the dentary. The maxillary fragments indicate that the palatine shelf is narrow and concave beneath, at least in the area ventral to the lachrymal bone.

These fossils are not like the bones of the other species represented in the Point Hodoul deposit. The general facies of the dentary (light build, closed Meckel's groove, rounded lingual surface and straight lower border) suggests gecko origin. Certainly, it does not resemble the dentary of any of the lygosomine skinks found in the area that were examined, although these also have closed Meckel's grooves. Among those checked was *Cryptoblepharus boutonii* (Desjardins, 1831), which occurs on Aldabra today. In this species, the dentary is considerably narrower latero-medially and the lingual face is more flattened than in the fossils.

Although the bones could not be precisely matched with any of the many West Indian Ocean and Ethiopian geckoes compared with them, they do have a general resemblance to the smaller species of *Phelsuma*. However, none of the members of this genus examined* have the mental foramina placed so close to the upper margin of the dentary. This feature and the very restricted taper of the cylindrical body of the bone distinguish the fossils from *P. abbotti*, which is now present on Aldabra.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. Possibly only one individual is represented.

ESTIMATED BODY SIZE. The very fragmented nature of the material makes this difficult to assess, but the remains probably come from a lizard not more than 50 mm from snout to vent.

Family IGUANIDAE
Iguanid lizards

Oplurus Cuvier, 1829

Bassin Cabri Calcarenites

MATERIAL REFERRED. *Registered number*: R8883–84. Maxilla: right – 3 incomplete sections (complete dental arcade, but nasal and palatine processes absent; section lacking most of dental arcade; posterior process with teeth). Dentary: right – 1 (short anterior section), left – 1 (posterior section). Isolated tooth – 1.

IDENTIFICATION. The maxilla with a complete dental arcade has a tooth-row that is about 21 mm long. The teeth are pleurodont and all, except the most anterior, have flattened, more or less trilobed crowns: the largest are about 4 mm

* Species of *Phelsuma* examined: *P. abbotti* Stejneger, 1893; *P. andamanensis* Blyth, 1860; *P. astriata* Tornier, 1901; *P. barbouri* Loveridge, 1942; *P. breviceps* Boettger, 1894; *P. cepediana* (Merrem, 1820); *P. dubia* (Boettger, 1881); *P. edwardnewtoni* Vinson & Vinson, 1969; *P. guentheri* Boulenger, 1885; *P. laticauda* (Boettger, 1880); *P. lineata* Gray, 1842; *P. madagascariensis* (Gray, 1831); *P. mutabilis* (Grandidier, 1869); *P. trilineata* Gray, 1842; *P. v-nigra* Boettger, 1913.

long. In the other, smaller, maxilla a well-developed, flat, triangular palatine process is present arising from about the middle of the bone. It is also apparent from the shape of the nasal process that the posterior border of the nasal orifice of the skull rose steeply. The two dentary fragments show that Meckel's groove is unclosed anteriorly and posteriorly although the middle section is not represented.

A pleurodont maxillary tooth-row of 21 mm is rare amongst present-day lizards of the Ethiopian region and the West Indian Ocean. Extant forms with maxillae approaching or exceeding this size include only monitors (*Varanus* Merrem, 1820) and large cordylids (*Gerrhosaurus* Wiegmann, 1828, *Zonosaurus* Boulenger, 1887), but these do not possess the trilobed teeth, fairly large palatine process and general habitus of the fossil material. The same is true of two recently extinct island lizards that grew large, the skink *Didosaurus mauritianus* Günther, 1877 of Mauritius and the gecko *Phelsuma gigas* (Liénard, 1842) of Rodriguez. Both of these also had fully closed Meckel's grooves. Modern relatives of the large Aldabra lizard must therefore be sought amongst smaller forms. In fact, the only species that have the characteristic features of the fossils are the members of the iguanid genus *Oplurus*, now known only from Madagascar and Grande Comore. The largest individual of the group examined in this study, an *O. cuvieri* 131 mm from snout to vent (BM 1930.7.1.149), has a maxillary tooth-row only 16·3 mm long.

No formal study of the interrelationships of the six species of *Oplurus* appears to have been made, but on superficial appearance they fall into two groups : (1) *O. quadrimaculatus* (Duméril, 1851), *O. saxicola* Grandidier, 1869 and the generally similar *O. fierinensis* Grandidier, 1869 and *O. grandidieri* (Mocquard, 1900) ; (2) *O. cuvieri* (Gray, 1831) – a senior synonym of *O. sebae* Duméril & Bibron, 1837 (see Savage, 1952) – and *O. cyclurus* (Merrem, 1820). The members of the first group have more flattened heads and bodies than those in the second and the species that have been examined here, viz. *quadrimaculatus* and *saxicola*, also differ from *cuvieri* and *cyclurus* in having a more concave lingual profile to the lateral cheek teeth and the maxillary border of the posterior edge of the external nasal opening of the skull curving more gently upwards. In the two latter features, the Aldabra maxillaries agree with *O. cuvieri* and *O. cyclurus*. The shape of the nasal process of the smaller maxillary and of its palatine process is much more like *cuvieri* than *cyclurus*, so on present limited evidence, the former species appears closest to the fossil material. At the present time, *O. cuvieri* occurs in West and Northwest Madagascar and on Grande Comore.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. As there are substantial fragments of two right maxillae that include homologous areas and are of different sizes, at least two individuals must be represented.

ESTIMATED BODY SIZE. The maxilla with teeth is about 21 mm long, while that of a modern *O. cuvieri* 131 mm from snout to vent is 16·3 mm. Making no allowance for allometric growth, this would suggest a snout to vent length for the lizard from which it came of about 170 mm. The smaller maxilla, on the basis of the same sort of calculation, might have come from an animal about 157 mm from snout to vent.

Point Hodoul cavity filling

MATERIAL REFERRED. *Registered number* : R8879-82. Maxilla : right – 1 fragment (short anterior section). Small tooth-bearing fragments : 4. Cervical vertebra : 1 (probably third or fourth). Dorsal vertebrae : fragment, 1 (probably from region immediately anterior to sacrum. This last specimen is the one referred to in Braithwaite *et al.* (1973) as 'possibly the vertebra of a varanid lizard'.)

IDENTIFICATION. This material is even more fragmentary than that from the Bassin Cabri Calcarenites, but again it is obvious that a large lizard with pleurodont, trilobed teeth is represented, the biggest teeth being 4·7 mm long. The remains correspond closely to *Oplurus*. The anterior section of the maxilla includes the premaxillary process, i.e. that part of the maxilla the superior surface of which forms the lower rim of the external nasal opening of the skull. This surface is concave and rises abruptly, medial to the anterior inferior alveolar foramen, to form a well developed ridge that declines anteriorly. This is similar to the condition found in *O. cyclurus* and particularly *O. cuvieri*. It is not like that present in the members of the *O. quadrimaculatus* group examined where the medial ridge is far less abrupt.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. The remains may only represent a single individual as none of the elements is duplicated, but see below.

ESTIMATED BODY SIZE. When compared with an *O. cuvieri* 125 mm from snout to vent, the linear dimensions of the fossil maxillary fragment were found to be about 1·7 to 1·8 times as great as the equivalent area of the modern individual while linear dimensions of the vertebrae were greater by a factor of over 2. This discrepancy might be due either to the maxilla and vertebrae coming from different individuals or, more probably, to negative allometric growth of the maxilla relative to the vertebrae. The measurements suggest that the *Oplurus* from the Point Hodoul cavity filling was probably at least 210 mm from snout to vent and possibly larger than 250 mm. *O. cuvieri* may have a tail length 1·7 times that of the body (Angel, 1942), so if the analogy to this species holds, the fossil lizard could have been between 570 and 680 mm in total length.

Differences from modern Oplurus cuvieri

Although the fossils agree best with *O. cuvieri* among living species of *Oplurus*, there are some distinct differences between them and modern material examined. Apart from their greater size, they differ in the following ways :

Bassin Cabri Calcarenites. The nasal process of the maxillary is more rugose with a rougher outer surface.

Point Hodoul cavity filling. 1. The anterior section of the maxilla has a very distinct ridge separating the superior and lateral surfaces of the premaxillary process ; this is markedly undercut anteriorly.

2. The cervical vertebra has the sagittal ridge running along the underside of the centrum very well developed and the area on each side of it much more concave than in *O. cuvieri*.

3. The dorsal vertebra has a distinct but ill defined ridge running transversely from the hind edge of the articular surface of each prezygopophysis towards the neural spine. This ridge accentuates the hollow between the leading edge of the neural arch and the prezygopopophysis.

As the Aldabra *Oplurus* was so much bigger than modern *O. cuvieri*, the differences might be expected to have an allometric component. However, when large and small examples of both *O. cuvieri* and *O. cyclurus* were examined, little evidence of the expected allometric trends could be found, although the sagittal ridge on the undersides of the third and fourth cervical vertebrae tends to become somewhat better developed. A series of the large iguanid, *Iguana iguana* (Linnaeus, 1758), also shows some limited change in the shape of the cervical vertebrae, but not in the other characters that distinguish the Aldabra *Oplurus* material. Since these features are well marked and there is no clear evidence that they include a large allometric component, it is possible that the fossils do represent a taxon distinguishable from modern *O. cuvieri*, but because the remains are so fragmentary, it seems unnecessary to give it formal recognition at the present time.

Family SCINCIDAE
Skinks
'*Scelotes* Fitzinger 1826'

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number* : R8799–8818. Maxillae : right – 5, left – 3. Prefrontals : right – 3, left – 1, Frontals : right – 8, left – 9. Parietals : 7. Conjoined vomers : 1. Pterygoids : right – 2, left – 2. Basioccipitals : 2 (one fragmentary). Quadrates : right – 6, left – 5. Dentaries : right – 19, left – 14. Proximal sections of mandibles : right – 9, left – 4. Axes : 3. Third cervical vertebrae : 2. Dorsal vertebrae : 223 approx. Sacra : 2. Basal caudal vertebrae : 2. Autotomic caudal vertebrae : 57 approx. Scapulocoracoid : right – 1. Pelvic girdles : right – 5, left – 3. Humeri : intact, left – 1 ; proximal sections, right – 4, left – 4 ; distal section, left – 1. Femora : intact, right – 2, left – 3 ; proximal sections, right – 4, left – 10 ; distal sections, right – 7, left – 3.

IDENTIFICATION. Dentaries in this sample are robust with Meckel's groove open throughout their lengths. The teeth are coarse, peg-like and pleurodont with crowns that are slightly compressed labio-lingually. In the largest specimens, about 18 teeth, or rather more, are present and the tooth-row is approximately 5·5 mm long. Among the lizards of the Ethiopian region and West Indian Ocean, pleurodonty rules out agamids and chameleons and size alone excludes varanids. The two iguanid genera in the area (*Oplurus* and *Chalarodon* Peters, 1854) have trilobed lateral teeth and partly closed Meckel's grooves. Geckoes can also be excluded as Meckel's groove is completely closed in this family. By elimination, it therefore seems probable that the mandibles are from a scincomorph lizard. This is supported by aspects of the associated remains, such as the even osteodermal layer on the frontals and parietals and the indications of large scales on the latter.

There are three scincomorph families in the area, namely the Lacertidae, Cordylidae and Scincidae. The fossils differ from members of the first two in the following ways :

1. The parietals have simple down-turned lateral edges, there being no tendency to extend laterally to form a partial roof over the supratemporal foramen.

2. In the midline area, the parietal projects backwards on each side of the *fossa parietalis* as two well developed and broadly separated processes.

3. The weakly indicated pattern of scales on the parietal osteodermal layer is unlike that of lacertids or cordylids.

However, all the features of the fossils occur in some Scincidae, so they have been assigned to this family.

Within the skinks, the material is quite unlike the aberrant Acontinae and Feylininae and differs from Ethiopian and West Indian Ocean Lygosominae examined in having an open Meckel's groove and paired frontals. Both these features are typical of the remaining subfamily, the Scincinae (Greer, 1970a). Scincinae of the Ethiopian region and the islands of the West Indian Ocean have been reviewed by Greer (1970b). This author states that a relatively small interparietal scale is confined to *Proscelotes* de Witte & Laurent, 1943 and to *Sepsina* Bocage, 1866 on the African mainland, and to the endemic scincines of the West Indian Ocean including Madagascar. The Aldabra material has a small interparietal scale indicated in the osteodermal layer of the parietal bone and, as it bears no close resemblance to *Proscelotes* or *Sepsina*, it seems reasonable to assume that it is nearest to the Indian Ocean forms. Of these, the species endemic to the Seychelles and Mascarene islands that were originally placed in *Scelotes* but are now assigned to separate genera can be eliminated from further consideration. All three, viz. *Gongylomorphus bojerii* (Desjardins, 1831), *Pamelaescincus gardinieri* (Boulenger, 1909) and *Janetaescincus braueri* (Boettger, 1896), have flatter parietals than the Aldabra specimens, with less lateral down-turning and at least a tendency to extend sideways over the supratemporal foramen. They also have much finer dentition. The remaining West Indian Ocean forms are confined to Madagascar and nearby islands (Glorioso and the Comores). The 39 or so nominal species have been assigned to a number of genera, the majority being placed in *Scelotes*. According to Greer, the whole group is in need of thorough revision and may not be particularly closely related to the *Scelotes* of the African mainland, which include the type species of the genus. The restricted understanding of the group, together with the fact that it is poorly represented in museum collections, precludes a comprehensive comparison with the Aldabra material, but the latter does seem very similar to the two medium-sized, short-legged populations that now occur respectively on the Comores and on Glorioso and are named as '*Scelotes*' *johannae* (Günther, 1880) and '*S.*' *valhallae* (Boulenger, 1909). The most obvious difference is that the Aldabra specimens have coarser dentition.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. On the basis of the commonest element present, the right mandible, at least 19 individuals are represented.

ESTIMATED BODY SIZE. Calculations based on the relative sizes of vertebrae, frontals, parietals and femora of the Aldabra material and of 'S.' *johannae* and 'S.' *valhallae* suggest that the largest Aldabra '*Scelotes*' in the sample grew to about 90 mm from snout to vent compared with at least 110 mm for 'S.' *johannae* and at least 104 mm for 'S.' *valhallae*.

Mabuya Fitzinger 1826

MATERIAL REFERRED. *Point Hodoul cavity filling. Registered number* : R8819–27. Maxillae : right – 2 (one with posterior tip missing, one with anterior section missing), left – 1 (anterior section missing). Frontals : 2 sections (posterior section, central section including left lateral flange). Jugal : right – 1. Quadrate : right–1. Dentary + splenial : left – 1 (posterior sections of bones and dentary tip absent). Dentary : left – 1 (middle section only). Articular section of mandible : right – 1. Dorsal vertebrae : 5. Humeri, proximal sections : right – 1, left – 1. Femur, distal section – 1.

IDENTIFICATION. The frontals are unpaired but their lateral flanges are not extended ventrally to form a tube, so they are unlikely to be of gecko origin. Both sections are covered dorsally by an even osteodermal layer and in the posterior one there are grooves representing the sutures between a large frontal scale and large paired frontoparietals, the suture between the latter being oblique. The general form of these frontals, their even osteodermal layer and the large scales indicated in it all suggest that they are from a scincomorph lizard. Cordylids can be discounted at once as they have paired frontals and this is also true of many lacertids, those showing the unpaired condition usually have the frontal quite strongly narrowed medially and the suture between the frontoparietal scales is more or less sagittal, not oblique. Neither of these features is present in the Aldabra material, so they are likely to belong to the remaining Old World scincomorph family, the Scincidae. According to Greer (1970a), only the Lygosominae among the skinks have unpaired frontals.

When the Aldabra material is compared with the lygosomines of the Ethiopian region and the West Indian Ocean, it is apparent that it agrees in detailed structure and proportion only with members of the genus *Mabuya*. This group has perhaps over 100 species distributed through Africa, southern Asia and central and southern America. About 50 of these are found in Africa and nearby islands and of these, 11 occur on islands in the West Indian Ocean including Madagascar. All species of *Mabuya* are generally similar, and many of them also tend to be intraspecifically variable in minor features, so a positive and exhaustive identification of fragmentary material would be extremely time-consuming, or, more probably, impossible. Therefore comparison here is restricted to the species already known from the West Indian Ocean.

Of the seven endemic Madagascan species, *M. gravenhorstii* (Duméril & Bibron, 1839) can be immediately excluded as it has fused frontoparietal scales. *M. elegans* (Peters, 1854) and the closely related *M. sakalava* (Grandidier, 1872) and *M. madagascariensis* Mocquard, 1908 differ from the Aldabra material in their smaller

size, very narrow frontal and thin osteodermal layer. Also, the nasal process of the maxilla is more curved in transverse section, and where it forms the anterior lower border of the orbit, the maxilla is reflected outwards, whereas in the Aldabra specimens it is not. With the exception of frontal width, *M. aureopunctata* (Grandidier, 1867) and *M. boettgeri* Boulenger, 1887 also differ from the Aldabra material in these respects. The remaining Madagascar species, the poorly known *M. betsileana* Mocquard, 1906, has not been examined.

Two closely related endemic species of *Mabuya* occur together on the Seychelles : *M. sechellensis* (Duméril & Bibron, 1839), which also reaches the Amirantes, and *M. wrightii* Boulenger, 1887. Both these differ from the Aldabra material in the shape of the maxilla : the anterior portion is more elongate and the upper part of the nasal process is more abruptly turned inwards.

On the Comores, two more species of *Mabuya* occur : the widespread East African *M. striata* (Peters, 1844) on Anjouan and *M. maculilabris* (Gray, 1845) on all the islands of the archipelago. The latter species is found right across tropical Africa. The Comores populations were originally described as a full species, *M. comorensis* (Peters, 1854), but they are now usually regarded as part of the *M. maculilabris* complex and are often considered as a subspecies in which some eastern African populations are also included. *M. striata* differs from the Aldabra material in having the upper edge of the maxilla reflected outwards where it forms the lower border of the orbit. *M. maculilabris*, on the other hand, matches the fossil fragments closely and they fall well within the range of variation encountered in this species. When compared with specimens from Anjouan (BM 77.8.9.1–10, the only Comores material easily available in this study) there is close correspondence in all fragments except the vertebrae. The fossils have the sagittal ridge on the underside of the centrum more marked than the recent specimens. However, at least some *M. maculilabris* from the African mainland (e.g. BM 1970.2134 – Moheli Peninsula, Tanzania ; 1970.2299 – Mombasa) have this feature as well developed as the fossils.

Thus, of the ten West Indian Ocean species of *Mabuya* investigated, the fossils agree best with *M. maculilabris*, which is the one that occurs geographically nearest to Aldabra at the present time.

ESTIMATED NUMBER OF INDIVIDUALS IN SAMPLE. The two portions of right maxillae include homologous sections, this is also true of the two dentary fragments. Therefore at least two individuals are represented.

ESTIMATED BODY SIZE. The largest maxilla compares closely with that of a *M. maculilabris* having a head about 20 mm long. This would suggest a snout to vent length of 80 to 95 mm, which is within the present size range of the species.

ORIGIN OF THE POINT HODOUL LIZARD DEPOSIT

The Point Hodoul lizard bones were found in a small solution cavity in the Aldabra limestone. Similar hollows nearby lacked fossil lizards, which might indicate that some factor had concentrated the remains. One possibility is that the cavity, in extended form previous to being reduced to its present size by erosion, acted as a

natural trap for lizards. But, if this were so, some lizards might still be expected to occur in similar cavities in the vicinity. Also, the geckoes, which make up a substantial proportion of the fossils, would have been efficient climbers with well developed adhesive toe-pads and it is difficult to envisage any sort of natural pitfall trap from which they would be unable to escape. Another possibility is that the remains represent the food residue of some predator. Such situations are known in the West Indies, where concentrations of the remains of small vertebrates in limestone caves and fissures have often been attributed to predation by owls (Anthony, 1919; Miller, 1929; Hecht, 1951; Etheridge, 1964, 1965, 1966). In these cases, there is sometimes strong circumstantial evidence in the form of associated owl bones (e.g. Wetmore, 1922; Etheridge, 1965 for Hispaniola: Etheridge, 1966 for New Providence). Furthermore, modern deposits of barn owl pellets in the West Indies frequently contain lizard remains (Wetmore & Swales, 1931; Hecht, 1951; Etheridge, 1965) and the kinds of lizards comprising these may occur in similar proportions to those found in some of the fossil deposits.

No owl bones, or those of any other obvious predator, were found in association with the Point Hodoul lizards but, in addition to their concentration, two other factors suggest that such an agent may have produced the deposit. Firstly, the sample shows a bias in the size of the lizards that constitute it, both very large and very small individuals being rare. The great majority have estimated snout to vent lengths of about 40 mm to 100 mm, only two individuals out of 57 (i.e. 3·5%) falling outside this range (see Table I). Yet the single *Oplurus* in the sample shows that lizards growing to over 200 mm were present on the island and extrapolation from modern forms suggests that lizards much smaller than 40 mm were at least sometimes abundant, since hatchlings of most of the species would have been well below this size (approximate hatching sizes of some modern forms related to the Point Hodoul lizards are as follows: *Geckolepis maculata*, 23 mm – Blanc, 1966; *Paroedura spp.*, 25 mm; *Mabuya maculilabris*, 25 mm). *A priori*, if the deposit represented a natural trap, a predominance of young lizards might be expected as these often wander much more than older animals, yet nearly all the remains are apparently from half-grown or adult individuals. It could be argued that paucity of very small lizards in the sample is due to greater fragility of their remains. This may be so, but at least some elements of the smaller animals present in the deposit are not much more fragmented than those of larger individuals, so the size distribution may not be artificial.

Secondly, a high proportion of the components of the deposit seem to represent nocturnal lizards. Modern *Paroedura* and *Geckolepis* are active at night or are crepuscular whereas *Oplurus*, *Mabuya* and *Phelsuma* (if it was indeed present) are all basically diurnal. Nothing is known about the times of activity of 'Scelotes' *johannae* and 'S.' *valhallae*, apparently the closest forms to the Aldabra 'Scelotes' population, although they too may be at least partly nocturnal. Many tropical and subtropical skinks are night-active and Mertens (1955) states that 'Scelotes' *splendidus* (Grandidier, 1872) of Madagascar, which is quite similar to 'S.' *johannae* and 'S.' *valhallae*, is strictly nocturnal in captivity. If 'Scelotes' is excluded, the ratio of nocturnal to diurnal individuals is 34 : 4 (89·5%), if it is counted as nocturnal the ratio is 53 : 4

TABLE I

Rough estimates of length (snout to vent) of individual lizards in the Point Hodoul deposit

Length (mm snout to vent)	30	40–50	51–60	61–80	81–100	100+	Basis for estimates
Paroedura	1	15	12				Frontals
Geckolepis			1		5		Humeri
? Phelsuma		1					Mandible
Oplurus						1	Maxilla and vertebrae
'Scelotes'				7	12		Mandibles
Mabuya					2		Maxillae
Number of individuals in each size class	1	16	13	7	19	1	Total = 57

As 'Scelotes' is much more slender than the other forms, a distribution based on weight rather than length would probably be more or less unimodal.

(93·0% nocturnal) and even if it is regarded as diurnal, nocturnal forms still pre-dominate 34 : 23 (59·7% nocturnal).

Limited size distribution and a high proportion of nocturnal animals would fit predation by an owl. In fact, apart from the single large *Oplurus* and the one juvenile *Paroedura*, both of which may not necessarily have been part of a predator food residue concentration, the size distribution of the Point Hodoul lizards is well within the limits recorded for West Indian owl deposits. While no owls are known from the fossil fauna of Aldabra and none are present now, the cosmopolitan barn owl, *Tyto alba* (Scopoli), was in residence there in 1906 (Benson & Penny, 1971). This species occurs on many quite isolated islands throughout much of the world and is thought to have been one of the agents that produced the West Indian deposits, so it might have produced the Aldabra concentration although some other species could have been responsible.

COMPARISON OF ALDABRA REPTILES WITH THOSE OF NEIGHBOURING AREAS

It is not possible to compare the extinct Aldabra reptiles with even roughly contemporaneous faunas in nearby areas for, with the exception of relatively late material from the Mascarenes, very few Quaternary reptile remains, especially those of lizards, are known from these regions. Table 2 shows the known Aldabra reptile fauna, past and present, and its distribution in neighbouring areas. It is apparent from this that Aldabra has more similarity to Madagascar and the Comores than to mainland East Africa and the Seychelles.

The Comores are thus the island group that shows most resemblance in its present fauna to the Point Hodoul fossil assemblage, which is not unexpected as this archi-pelago lies less than 400 km from Aldabra. However, the Comores have a number of forms that are unrepresented in the fossil material or indeed in the extant fauna of the atoll. Thus, there are up to three species of *Phelsuma* on each island and on one or more of them occurs the small gecko, *Ebanavia inunguis* Boettger, 1878, chameleons, the skink, *Mabuya striata*, and up to three species of snake. It cannot be ruled out that some of these forms were present on Aldabra when the Point Hodoul deposits were being laid down, for the sample of fossil lizards is very likely not to be fully representative. It is small, consisting of a minimum of 57 individuals, and of the six species present three could be represented by only one, one and two individuals respectively. Even assuming that the remains were randomly accumulated, sampling error alone might have excluded some species. In fact, random accumulation is most improbable, for even a wide-ranging predator is unlikely to have hunted evenly over all habitats of the atoll and, as has been shown, small forms and diurnal ones are under-represented. So, if minute lizards like *Ebanavia* and diurnal forms like chameleons and additional species of *Phelsuma* were present, they might well have been excluded from the sample. For the same reasons, the possibility cannot be discounted that the tiny diurnal skink, *Crypto-blepharus boutoni*, now on the atoll may have been present when the Point Hodoul deposit was formed. The extant gecko, *Hemidactylus mercatorius* Gray, 1842, on

TABLE 2

The known Aldabra reptile fauna and its distribution in neighbouring areas

	Aldabra	Comores	Madagascar	Seychelles	Mainland E. Africa
Geochelone (Aldabrachelys)	*	+?	+	+	*
Crocodylus niloticus	+	*	*	+	
Paroedura	+	*	*		
Geckolepis maculata etc.	+?/*	*	*	*	
Phelsuma	*	*	*	*	
Hemidactylus mercatorius	+	*	*	*	*
Ophurus cuvieri etc.	+	*	*		
'Scelotes' johannae etc.	+	*	other Mabuya spp.	other Mabuya spp.	*
Mabuya maculilabris etc.			*	*	*
Cryptoblepharus boutonii	*	*			

*–present. +–known to have occurred in the Quaternary but extinct now. ?–occurrence uncertain.

the other hand is about the same size as the well represented fossil *Paroedura*, probably occupies similar habitats and, like this species, is basically nocturnal, so its absence from the deposit might indicate that it was not on Aldabra when this was laid down.

HABITAT REQUIREMENTS OF EXTINCT ALDABRA REPTILES

Speculating about past vegetation and climate on the basis of the ecological requirements of modern forms that are represented in fossil deposits is a hazardous exercise. This is especially true in the present case, for some of the fossil populations were rather different from the most similar extant forms and it is impossible to be certain that their requirements would have been the same, especially as reptiles colonizing small islands often seem to survive in rather different conditions from those in which their parent populations lived. Such speculation is made more difficult because very little is still known about the basic ecological needs of most West Indian Ocean reptiles. The relevant information that can be assembled is summarized below :

1. Giant tortoises. Recent giant tortoises of the West Indian Ocean, *Geochelone* (sub-genera *Aldabrachelys*, and *Cylindraspis*) have occurred within historical times both on relatively dry, low islands like Aldabra and on better watered, higher ones like Mahé, Mauritius and Rodriguez. It seems likely, therefore, that they are tolerant of a fairly wide range of conditions.

2. *Crocodylus niloticus*. Although most populations live in fresh water, this species can survive in coastal mangrove associations, as it does on parts of the East African seaboard. However, it does not usually occur on bare sea beaches.

3. *Paroedura stumpffi* group. Very little is known about the requirements of any *Paroedura* species, although they normally seem to occur in rather dry habitats and are apparently not closely associated with trees. Virtually nothing appears to have been written about the ecology of *P. sanctijohannis* or *P. stumpffi*. The type of *P. homalorhina* was collected at the entrance to a cave (Angel, 1936), but *P. androyensis*, *P. picta* and *P. bastardi* are recorded from rocky surfaces near the sea (Angel, 1942) and the latter species is also found in semidesert 'brushwood' areas (Angel, 1942 ; field notes by C. J. Inchley attached to BM 1967.55–67). Blanc & Blanc (1967) also found this species under slabs on rock pavements in deforested mountain areas.

4. *Geckolepis*. The members of this genus seem often to live on the trunks of trees. Angel (1942) records *G. maculata* from crevices in tree trunks and Blanc (1966) found it with *G. typica* in stands of trees with epiphyte-covered boles.

5. *Oplurus cuvieri*. This species is said by Angel (1942) to occur in 'steppe' country in dry places but, as he says that it may be seen on the trunks of trees, it seems probable that it is not confined to really arid areas.

6. 'Scelotes' nr. *johannae*. Madagascan 'Scelotes', although all superficially similar in form and all probably basically ground dwelling and rather cryptic, appear to be very varied in their habitat. Thus, some like 'S.' *igneocaudatus* (Grandidier, 1867)

may be found in semidesert (Angel, 1942), while others, e.g. 'S' *astrolabi* (Duméril & Bibron, 1839) and 'S.' *gastrostictus* (O'Shaughnessy, 1879) are partly aquatic (Millot, 1951 ; Paulian, 1953). Nothing much is known about 'S.' *johannae*. The types were taken under stones in a sugar plantation on the well vegetated island of Anjouan (Günther, 1880) and another specimen from Moheli (BM 1975.2072) was collected 'under leaf litter of *Terminalia*' by J. Frazier.

7. *Mabuya maculilabris*. Loveridge (1957) states that the East African populations that he refers to *M. m. comorensis* are confined to 'chiefly virgin forest or recently deforested areas' of Kenya and Tanzania. In other regions of mainland Africa, the species apparently occurs in both forest and savannah. On Europa island, it is mainly ground-dwelling but sometimes climbs on tree boles (Brygoo, 1966) and on Moheli, in the Comores, it is often associated with coconut palms, which it may climb to the crown (A. Cheke – personal communication).

It is impossible to gain much idea from the reptile remains of the conditions obtaining when the Bassin Cabri Calcarenites were laid down. Only three species are known from these deposits and of these, one is tolerant of a wide range of conditions (*Geochelone*) and the precise ecological requirements of another (*Oplurus*) are not really known. All that can be said is that the presence of *Crocodylus* suggests that mangroves may have been present near Bassin Cabri at this time.

The fact that the reptiles in the Point Hodoul cavity fillings are like the present Comores fauna may indicate that the deposits were produced at a time when conditions were like those now occurring in that archipelago, which has a higher rainfall and more abundant vegetation than Aldabra. This is supported to some extent by the known habits of *Geckolepis maculata* and *Mabuya maculilabris*, both of which seem to be often associated with large trees ; these are not abundant on Aldabra today. The presence of *Crocodylus* at Point Hodoul may indicate that mangrove then occurred on the outer (seaward) edge of the atoll where it is now absent.

POSSIBLE RESOURCE PARTITION BY EXTINCT ALDABRA REPTILES

The six genera of lizards in the Point Hodoul deposit occur together at the present time on Madagascar and on the high, medium-sized island of Grande Comore,* but they are not now found on any small, low island like Aldabra. As both Madagascar and Grande Comore support a wider range of environments than Aldabra ever could, the possibility is raised that the six forms might not have occurred exactly simultaneously on Aldabra. It is therefore worth enquiring whether any of them are so similar in their salient ecological parameters that occupation of quite separate habitats would be necessary to avoid severe competition.

Sympatric lizard species usually partition the resources of their environment on the following bases : temporal separation, differences in habitat or microhabitat, active selection of different sizes of prey and, more rarely, selection of different food *types*. In warm areas, the most obvious temporal separation is into diurnal and

* The other Comores islands have five of the genera, but lack *Oplurus*. Blanc (1972) indicates that they all lack *Geckolepis* too and that Grande Comore has no *Paroedura*, but this seems to be erroneous for the Musée Nationale d'Histoire Naturelle, Paris, has a specimen of *Geckolepis maculata* from Mayotte (PM 87.26) and seven *Paroedura sanctijohannis* from Grande Comore (PM 90.14–20).

TABLE 3

Point Hodoul lizard fauna : likely differences in ecologically important parameters

	Probable main period of activity	Approx. maximum head length (mm)	Likely diet	Probable climbing ability	Probable habitat
Pavoedura	night	20	invertebrates	good	not typically on trees
Geckolepis	night	27	invertebrates	very good	often on tree boles
'Scelotes'	uncertain	15	invertebrates	very poor	ground-dwelling, probably cryptic in litter etc.
Phelsuma (if present)	day	13	invertebrates	very good	scansorial on various surfaces
Mabuya	day	20	invertebrates	good	ground, also tree boles
Oplurus	day	60+	small animals and vegetation	good ?	ground, also tree boles

nocturnal forms. Habitat differences are often based on variations in insolation, humidity and substrate (e.g. ground type, whether more or less horizontal or vertical surfaces are preferred and, if the latter, whether they are trees, rock faces etc.). As most lizards are general predators, food size is often a more important parameter in reducing competition than food type, although a minority of species are specialists taking high proportions of, for instance, vegetation, ants or small vertebrates.

As stated, not much information is available about the habits of the modern relatives of the members of the Point Hodoul fauna. But what little there is can be augmented by various means, including examination of stomach contents (for dietary differences), speculation based on their morphology and analogies drawn from related forms. Thus, lizard head length often correlates with the size of prey usually eaten, well developed toe-pads in geckoes typically indicate good climbing ability, and large corneas and vertically slit-shaped pupils suggest at least partial nocturnality. Potentially important differences between the Point Hodoul lizards are given in Table 3. From this it can be seen that members of any pair of species may well have differed in at least one parameter of probable ecological significance and usually in more. So, it is unlikely that any of them would have been precise ecological equivalents and there is no reason to think that they could not have coexisted, assuming of course that the atoll supported the minimum microhabitat diversity to allow this.

BODY SIZE AND 'ISLAND GIGANTISM'

The most striking differences between the Point Hodoul lizards and their modern relatives are in apparent maximum size. Thus the linear dimensions of the *Oplurus* may have been almost twice those of the largest living member of the genus and the *Geckolepis* was about 30% longer than the largest species alive today. The *Paroedura* and '*Scelotes*', on the other hand, may have been somewhat smaller than their extant relatives.

A general tendency to large body size in a number of lizard and other groups on small islands is often given formal recognition in the literature as 'island gigantism'. Certainly, in many of the more important lizard families some of the largest forms (although not all) occur on small islands. This is true for geckoes, iguanids, lacertids, skinks and varanids and a similar trend is apparent in land tortoises. One probable reason for this is that many reptiles are much better transmarine colonizers than most mammals and are better at surviving transient periods of adverse conditions. Consequently they often get to, and persist on, small islands where the relatively large mammals that would normally occupy predator and vegetarian niches in mainland areas are entirely absent. The reptiles can therefore expand into this vacant ecological space with consequent increase in body size (or if they were large to start with, without reduction). Very large lizards occur, or have quite recently occurred, on at least five islands or island groups in the African region (see Table 4). Significantly, four out of the five giant forms involved are, or were probably, substantially vegetarian (viz. *Gallotia*, *Macroscincus*, *Phelsuma gigas* and, by analogy with its living relatives, the Aldabra *Oplurus* ; the diet of *Didosaurus* is uncertain).

TABLE 4

Giant lizards on small islands in the African region

Island	Giant form	Family	Maximum size, snout to vent (mm)	Largest related forms in possible source area, or on nearby mainland or large island	Maximum size, snout to vent (mm)	Other forms on same island
W. Canaries	*Gallotia* (*G. goliath*,† *G. simonyi* etc.)	Lacertidae	400+ estimated	*Lacerta lepida* (S.W. Europe, N.W. Africa)	210	Geckoes (*Tarentola*) Skinks (*Chalcides*)
Ilheo Branco and I. Razo, Cape Verde Is	*Macroscincus coctei* (apparently a huge *Mabuya* – see e.g. Greer, in press)	Scincidae	320	*Mabuya perroteti* (West Africa)	150	Geckoes (*Tarentola*) Skinks (*Mabuya*)
Aldabra	*Oplurus* sp.†	Iguanidae	210 – 250+ estimated	*Oplurus cuvieri* (Madagascar and Comores)	132	Geckoes (see text) Skinks (see text)
Mauritius	*Didosaurus mauritianus*†	Scincidae	300 estimated	Members of Group II of the *Leiolopisma* assemblage (Greer, 1974) (East Indies)	80*	Geckoes (e.g. *Phelsuma*) Skinks (e.g. *Gongylomorphus*)
Rodriguez	*Phelsuma gigas*†	Gekkonidae	220 estimated	*P. madagascariensis* (Madagascar etc.)	120	Geckoes (e.g. *Phelsuma*)

* but up to 288 mm on some small islands.
† extinct species.

Yet, although this habit is not uncommon in iguanids, it is not, or only weakly, developed in mainland geckoes, skinks and lacertids.

It is also noteworthy that none of the five giants in Table 4 are closely related to each other, even when they occur on neighbouring islands that were probably colonized from the same general source area as with Mauritius and Rodriguez. This indicates that the ability to produce giants is widespread amongst lizards, but possibly once a large form has developed on a small island, its presence inhibits the development of further giants. This is supported by the fact that, in the listed examples, other species coexist with the giants but have not become large, even when they are members of groups that have produced giants elsewhere (the *Mabuya* stock including *Macroscincus, Phelsuma*).

Evolution and maintenance of size differences seem to be common phenomena in island lizards, for instance Schoener (1970) found that *Anolis* (Iguanidae) species in the West Indies often diverge in body size when sympatric. Such differences may be particularly marked on small islands because restricted habitat diversity limits the extent to which species can partition resources by the selection of different microhabitats and therefore increases the need to evolve differences in prey size and hence body size. The large apparent size difference between the two probably nocturnal geckoes in the Point Hodoul cavity filling may be a case in point. Here, *Paroedura* seems to have grown to about 60 mm snout to vent, while *Geckolepis* attained 90 to 100 mm. On the Comores and on Madagascar, members of these two genera do occur together with wide overlap of size, but it is certain that these localities provide a wider range of environments than Aldabra did, so evolution of clear size differences has not been necessary.

As might be expected from experience with domestic animals, size in vertebrates is often very labile and easily modified by selection. Certainly in lizards the body size of populations may vary quite extensively through time. For instance Etheridge (1964, 1965, 1966) found that in the West Indies the body size of several species was considerably less than that of presumed ancestral fossil populations on the same island.

POSSIBLE CAUSES OF EXTINCTION

Although one cannot be sure that none of the present lizards of Aldabra was on the atoll when the Bassin Cabri Calcarenites and the Point Hodoul deposits were formed, it is certain that the crocodile and the six lizards represented in them are now extinct on the island. Among possible reasons for their disappearance are: (1) competitive exclusion by forms now present on the island; (2) extermination by an invading predator; and (3) transient or permanent loss of essential ecological resources.

Competitive exclusion

If the three present Aldabra lizards arrived after the Point Hodoul deposit was formed, it is possible that they could have displaced some of the species represented

in it.   However, in a stable situation, with no accompanying changes in ecological resources, this would only be likely to happen if the ecological space required by the invader more or less completely overlapped that of one or more of the species already there.   Also, in a stable situation, an island lizard is quite likely to be better adapted to its immediate environment than one coming from elsewhere.   This, together with the fact that an invader would be initially greatly outnumbered and would just have completed a debilitating transmarine journey, should give the original inhabitant great advantages over potential competitors arriving from outside.   If, on the other hand, the island environment was undergoing change at the time of invasion in a way that favoured the incursor, then replacement would be more likely.

It is possible that *Hemidactylus mercatorius* has roughly the same requirements as the Aldabra *Paroedura* (see p. 104) and *Phelsuma abbotti* might be the ecological equivalent of the putative *Phelsuma* in the Point Hodoul deposits.   The third species now on Aldabra, the skink *Cryptoblepharus boutonii*, is too small to have been a competitor of either of the fossil skinks, unless of course it competed with their young.   But this is not very likely, especially as it is known that *Cryptoblepharus* can coexist on small islands with forms identical with, or very similar to, the fossils : it occurs with *Mabuya maculilabris* on Europa and with 'Scelotes' valhallae on Glorioso.   So, the present species would only have been likely to displace at most two of the six Point Hodoul lizards.

Extermination by an invading predator

On small islands, introduced predators often destroy a high proportion of indigenous reptiles.   Mongooses and rats were probably responsible for the extermination of many endemic West Indian populations and a similar process seems to have taken place on Rodriguez and Mauritius, the former island having lost its two native geckoes.   Ten endemic Mascarene reptile species probably occurred on Mauritius of which six are no longer found on the main island and a seventh is apparently restricted to a single locality there (for the lizards, see Vinson & Vinson, 1969, and Vinson, 1973).   Habitat destruction may have contributed, but it does not seem to have been the main factor, for five of the forms now extinct on Mauritius itself still survive on offshore islands that are free of mammalian predators even though the natural vegetation is greatly reduced.   In such cases, the predators concerned are ones with a broad dietary tolerance, so that a fall in numbers of a particular prey-type does not produce a corresponding drop in predator numbers through starvation.   Consequently, predator pressure on a declining species is not reduced. Presumably, island endemics are exterminated because they lack the requisite antipredator strategies to resist an invader and, as the numbers of individuals and their range is restricted, they are hunted out swiftly, before these can evolve.

One can envisage a natural situation like this with perhaps an avian predator arriving on an isolated small island like Aldabra.   As has been suggested, owls may have been active when the Point Hodoul deposit was formed and rats have reached the island since (presumably by human agency).   Both of these might have been capable of reducing the fauna, but it is very difficult to assess their actual importance.

Loss of ecological resources

It is likely that the number of forms an island can support is partly dependent on habitat diversity. Reduction in diversity, even transiently, may mean that some species would not survive. Such reduction may have occurred on Aldabra. For instance, the presence of *Geckolepis* and *Mabuya* nr. *maculilabris* in the Point Hodoul deposit suggests that large trees may have been more abundant at this time ; reduction or temporary complete loss of these could have hazarded the lizards. However, it is not easy to see why so many of the fossil forms disappeared. One possibility is that the island suffered a transient period of very adverse conditions, for instance an extended drought. Such an event seems quite possible in the varying climatic conditions of the late Quaternary. A low atoll like Aldabra would be more prone to extreme drought than high islands like the Comores where orographic influences probably produced a more stable rainfall. These islands still possess a fauna similar to that represented in the Point Hodoul deposits. In the West Indian Ocean, low islands certainly seem more prone to extinction of their faunas, for their level of endemicity is much lower than that on high islands (Peake, 1971). Braithwaite *et al.* (1973) suggest that the breaching of the Aldabra land rim and the flooding of the lagoon, which took place perhaps 4000 to 5000 years ago and reduced the area of the island by 60%, may have been responsible for widespread destruction of habitat and consequent extermination. Whether one or both these factors were responsible, permanent or transient loss of ecological resources seems a likely primary cause of the extinction of the Point Hodoul reptile fauna. Even if competitive replacement was also involved it would have been most likely to take place in such a changing environment.

COLONIZING ABILITY OF ALDABRA REPTILES

It is virtually certain that Aldabra received its reptiles by transmarine migration (although one or more of the modern species might possibly have been transported by man), so one would expect the forms that reached the atoll to have been well adapted to the hazards of sea crossings and the perilous early stages of colonization. There is some circumstantial evidence that this is so. One indication is that all the reptile groups known from Aldabra have got to at least one other oceanic island that would have required a transmarine journey. *Paroedura*, *Geckolepis* and *Oplurus* are all on the Comores, *Mabuya* and *Crocodylus* reached this archipelago and the Seychelles as well, and the other groups (if '*Scelotes*' is taken to include the endemic scincines of Mauritius and the Seychelles) got to a relatively large number of islands in the West Indian Ocean.

Aldabra has probably been completely submerged twice during its occupation by giant tortoises, which would imply that they colonized the atoll not once but three times (Braithwaite *et al.*, 1973). Similarly, remains of *Crocodylus* and *Oplurus* occur in both the Bassin Cabri Calcarenites and the Point Hodoul cavity fillings. These deposits are separated by the marine Aldabra limestone, so the reptiles common to them must have colonized at least twice.

In the West Indies, the species of the iguanid genus *Anolis* that are successful colonizers are all typical of savannah or open forest situations, none of them being mainly rain forest or montane forms (Williams, 1969). Wilson (1959, 1961) has found an analogous situation in Melanesian ants. With the exception of the crocodile, the reptiles that have reached Aldabra fit this pattern. All those in which habits are known or can be guessed would be expected to occur at least sometimes in fairly dry habitats, such as littoral situations (in the case of *Cryptoblepharus*) or savannah. This is true even of the probably tree-associated forms, *Geckolepis* and *Mabuya* nr. *maculilabris*. Williams thinks that this general trend results from the greater ability of dry-adapted animals to survive the almost inevitable desiccation of a sea passage.

Another characteristic to be expected in successful colonizers is the ability to swim, or float, or cling to rafting vegetation. *Crocodylus niloticus* sometimes lives permanently in coastal areas and is obviously well fitted for survival at sea, and giant tortoises are known to float well (see e.g. Grubb, 1971). Virtually all the Aldabra lizards have, or had, good climbing ability and consequently might be expected to maintain their position well on floating objects. The only exception is the very short-legged, probably ground-dwelling 'Scelotes'.

Parthenogenesis is obviously an initial advantage in a colonizing species since any individual of an all-female species, irrespective of age, can form a propagule. Some of the most widespread species of oceanic reptiles seem to be parthenogenetic including the worm snake, *Ramphotyphlops braminus* (Daudin, 1803) – McDowell, 1974, and the gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836) – Gorman, 1973, but all four reptile species on Aldabra at the present time are bisexual and none of the fossil forms belong to genera in which parthenogenesis has been reported.

REFERENCES

ANGEL, F. 1936. Deux gekkos nouveaux de Madagascar appartenant au genre *Phyllodactylus*. *Bull. Soc. zool. Fr.* **61** : 508–511.
—— 1942. Les lézards de Madagascar. *Mem. Acad. malagache*, **36** : 1–193.
ANTHONY, H. E. 1919. Mammals collected in eastern Cuba in 1917, with descriptions of two new species. *Bull. Am. Mus. nat. Hist.* **41** : 625–643.
BELLAIRS, A. D'A. 1969. *The life of reptiles, vol. II.* London.

BENSON, C. W. & PENNY, M. J. 1971. The land birds of Aldabra. *Phil. Trans. R. Soc. B.* **260** : 417–527.

BLANC, C. P. 1966. Notes sur les Gekkonidae de Madagascar : I – Observations relatives à deux espèces de *Geckolepis* : *G. maculata* Peters, 1880 et *G. typica* Grandidier, 1867. *Vie Milieu,* **17** : 453–460.

—— 1972. Les reptiles de Madagascar et des îles voisines. *In* Battistini, R. & Richard-Vindard, G. (eds), *Biogeography and ecology in Madagascar* : 501–614. The Hague.

—— & BLANC, C. F. 1967. Observations écologiques sur les Sauriens du Mont Bity. *Ann. Univ. Madag. (Série Sci. Nat. Mat.),* **5** : 67–74.

BRAITHWAITE, C. J. R., TAYLOR, J. D. & KENNEDY, W. J. 1973. The evolution of an atoll : the depositional and erosional history of Aldabra. *Phil. Trans. R. Soc. B,* **266** : 307–340.

BRAVO, T. 1953. *Lacerta maxima* n. sp. de la fauna extinguida en el Pleistoceno de las Islas Canarias. *Estudios geol. Inst. Invest. geol. Lucas Mallada,* **9** : 7–34.

BRYGOO, E. R. 1966. Note sur les reptiles terrestres récoltés à Europa en Avril 1964. *Mem. Mus. natn. Hist. nat. Paris (Série A),* **41** : 29–31.

COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. zool. Soc. Lond.* **29** (4) : 211–350.

DIXON, J. R. & KROLL, J. C. 1974. Resurrection of the generic name *Paroedura* for the phyllodactyline geckoes of Madagascar, and a description of a new species. *Copeia,* **1974** (1) : 24–30.

ETHERIDGE, R. 1964. Late Pleistocene lizards from Barbuda, British West Indies. *Bull. Fla St. Mus. biol. Sci.* **9** (2) : 43–75.

—— 1965. Fossil lizards from the Dominican Republic. *Q. Jl Fla Acad. Sci.* **28** (1) : 83–105.

—— 1966. Pleistocene lizards from New Providence. *Q. Jl Fla Acad. Sci.* **28** (4) : 349–358.

GORMAN, G. C. 1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. *In* Chiarelli, A. B. & Capanna, E. (eds), *Cytotaxonomy and vertebrate evolution* : 349–424.

GREER, A. E. 1970a. A subfamilial classification of scincid lizards. *Bull. Mus. comp. Zool. Harv.* **139** (3) : 151–183.

—— 1970b. The systematics and evolution of the subsaharan Africa, Seychelles and Mauritius scincine scincid lizards. *Bull. Mus. comp. Zool. Harv.* **140** (1) : 1–23.

—— 1974. The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Aust. J. Zool.* Supplementary series **31** : 1–67.

—— (in press). On the evolution of the giant Cape Verdes scincid lizard *Macroscincus coctei*. *J. nat. Hist.*

GRUBB, P. 1971. The growth, ecology and population structure of giant tortoises on Aldabra. *Phil. Trans. R. Soc. B.* **260** : 327–372.

GÜNTHER, A. 1879. On mammals and reptiles from Johanna, Comoro Islands. *Ann. Mag. nat. Hist.* (5) **3** : 215–219.

—— 1880. Description of new species of reptiles from Eastern Africa. *Ann. Mag. nat. Hist.* (5) **6** : 234–238.

HECHT, M. K. 1951. Fossil lizards of the West Indian genus *Aristelliger* (Gekkonidae). *Am. Mus. Novit.* **1538** : 1–33.

LOVERIDGE, A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda ; Kenya ; Tanganyika ; Zanzibar). *Bull. Mus. comp. Zool. Harv.* **117** (2) : 153–362.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton, New Jersey.

McDOWELL, S. B. 1974. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum, part I. Scolecophidia. *J. Herpetol.* **8** (1) : 1–57.

MERTENS, R. 1955. Studien über die Reptilienfauna Madagaskars, I. Beobachtungen an einigen madagassischen Reptilien im Leben. *Zool. Gart. Lpz.* **22** : 57–73.

MILLER, G. S. 1929. A second collection of mammals from caves near St. Michel, Haiti. *Smithson. misc. Collns,* **74** (3) : 1–8.

MILLOT, J.   1951.   Un lézard d'eau à Madagascar (*Scelotes astrolabi* Dum. et Bib.).   *Naturaliste malagache*, **3** : 87–90.

OELRICH, T. M.   1956.   The anatomy of the head of *Ctenosaura pectinata* (Iguanidae).   *Misc. Publs Mus. Zool. Univ. Mich.* **94** : 1–122.

PAULIAN, R.   1953.   A propos des lézards aquatiques.   *Naturaliste malagache*, **5** : 108.

PEAKE, J. F.   1971.   The evolution of terrestrial faunas in the Western Indian Ocean.   *Phil. Trans. R. Soc. B*, **260** : 581–610.

SAVAGE, J.   1952.   The correct generic names for the iguanid lizards of Madagascar and the Fiji islands.   *Copeia*, **1952** (3) : 182.

SCHOENER, T. W.   1970.   Size patterns in West Indian *Anolis* lizards. II.   Correlations with the sizes of particular sympatric species – displacement and convergence.   *Am. Nat.* **104** : 155–173.

THOMPSON, J. & WALTON, A.   1972.   Redetermination in the chronology of Aldabra Atoll by ^{230}Th/^{234}U dating.   *Nature, Lond.* **240** : 145–146.

VINSON, J. & VINSON, J.-M.   1969.   The saurian fauna of the Mascarene Islands.   *Bull. Mauritius Inst.* **6** (4) : 203–320.

VINSON, J.-M.   1973.   A new skink of the genus *Gongylomorphus* from the Macabé Forest (Mauritius).   *Revue agric. sucr. Île Maurice*, **52** : 39–40.

WETMORE, A.   1922.   Remains of birds from caves in the Republic of Haiti.   *Smithson. misc. Collns*, **74** (4) : 1–4.

—— & SWALES, B. H.   1931.   The birds of Haiti and the Dominican Republic.   *Bull. U.S. natn. Mus.* **155** : 234–236.

WILLIAMS, E. E.   1969.   The ecology of colonisation as seen in the zoogeography of anoline lizards on small islands.   *Q. Rev. Biol.* **44** (4) : 345–389.

WILSON, E. O.   1959.   Adaptive shift and dispersal in a tropical ant fauna.   *Evolution, Lancaster, Pa*, **13** : 122–144.

—— 1961.   The nature of the taxon cycle in the Melanesian ant fauna.   *Am. Nat.* **95** : 169–193.

E. N. ARNOLD D. Phil.
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD